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LETTER

Biomass estimation in mangrove forests: a comparison of allometric models incorporating species and structural information

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Supplementary material for this article is available online

Abstract

Improved estimates of aboveground biomass (AGB) are required to improve our understanding of the productivity of mangrove forests to support the long-term conservation of these fragile ecosystems which are under threat from many natural and anthropogenic pressures. To understand how individual species affects biomass estimates in mangrove forests, five species-specific and four genus-specific allometric models were developed. Independent tree inventory data were collected from 140 sample plots to compare the AGB among the species-specific models and seven frequently used pan-tropical and Sundarbans-specific generic models. The effect of individual tree species was also evaluated using model parameters for wood densities (from individual trees to the whole Sundarbans) and tree heights (individual, plot average and plot top height). All nine developed models explained a high percentage of the variance in tree AGB ($R^2 = 0.97$–0.99) with the diameter at breast height and total height (H). At the individual tree level, the generic allometric models overestimated AGB from 22% to 167% compared to the species-specific models. At the plot level, mean AGB varied from 111.36 Mg ha^{-1} to 299.48 Mg ha^{-1}, where AGB significantly differed in all generic models compared to the species-specific models ($p < 0.05$). Using measured species wood density (WD) in the allometric model showed 4.5%–9.7% less biomass than WD from published databases and other sources. When using plot top height and plot average height rather than measured individual tree height, the AGB was overestimated by 19.5% and underestimated by 8.3% ($p < 0.05$). The study demonstrates that species-specific allometric models and individual tree measurements benefit biomass estimation in mangrove forests. Tree level measurement from the inventory plots, if available, should be included in allometric models to improve the accuracy of forest biomass estimates, particularly when upscaling individual trees up to the ecosystem level.

1. Introduction

There has been a global effort to develop accurate and efficient methods to quantify aboveground carbon (measured as biomass) in mangrove forests (Hutchison *et al* 2014, Ni-Meister 2015, Baccini *et al* 2017, Lagomasino *et al* 2019). A range of remote sensing (RS) technologies can indirectly infer forest biomass but field data are needed to calibrate and validate products (Gibbs *et al* 2007, Chave *et al* 2019, Réjou-Méchain *et al* 2019). Destructive harvesting of trees provides the most precise estimates of aboveground biomass (AGB), yet is impractical, laborious, costly and often illegal (Komiyama *et al* 2008, Edwards *et al* 2019) and so mathematical models have been developed to estimate tree biomass from easily measured biophysical parameters (tree diameter at breast height (DBH), height (H), or wood density (WD)) (Brown 1997, Komiyama *et al* 2005, Picard *et al* 2012, Chave *et al* 2014). These models are known as allometric models. However, this method of estimation can yield a large degree of uncertainty scaling up from individual tree biomass to plot and forest-level as uncertainties associated with individual trees are propagated (van Breugel *et al* 2011, Petrokofsky *et al* 2012, Réjou-Méchain *et al* 2019). The choice of appropriate allometric model is therefore critical to reduce uncertainties in the estimation of forest biomass.

All allometric models have limitations since they are based on a limited number of destructively sampled trees and often the sample locations are unrepresentative of forest heterogeneity (Weiskittel *et al* 2015, Hickey *et al* 2018). These models also introduce an uncertainty when applied to species without the destructive sample (Mitchard *et al* 2013, Ngomanda *et al* 2014, Mahmood *et al* 2019). For example, de Souza Pereira *et al* (2018) found AGB estimation errors between minus 18% and plus 14% when using biome-specific allometries rather than species-specific ones in Brazilian mangrove forests. On the other hand, a few studies have shown that generic models can outcompete locally developed ones (Rutishauser *et al* 2013, Stas *et al* 2017). Uncertainties also arise from inappropriate use of regression models without considering collinearity of parameters, uncritical use of model dredging and inappropriate criteria for model selection (Sileshi 2014, Vorster *et al* 2020). Recently published global and continental AGB estimates contain errors due to an under representative sample size and the exclusion of the climatic regime, geophysical and geomorphological variables, which are key to understanding the spatial distribution of biomass (Rovai *et al* 2016). Inclusion of biophysical parameters such as WD and tree height can help to capture geographical heterogeneity and also act as a suitable proxy of environmental drivers such as variation in salinity which affects the growth rate, WD, species composition and tree height (Mahmood *et al* 2019, Rahman *et al* 2020, 2021, Virgulino-Júnior *et al* 2020).

Although WD is an important variable for assessing carbon content, it is rarely measured during field inventories. Most studies identify species and then use published WD values from a database of generic values (Njana *et al* 2016, Réjou-Méchain *et al* 2019). Using the same, or grouped, WD in the allometric model tends to smooth species-level variations in AGB (Mitchard *et al* 2013, Ni-Meister 2015). The inclusion of tree height has a large effect on individual tree and forest AGB (Feldpausch *et al* 2012). Any errors introduced during individual tree height measurements can originate from the choice of methods and/or instruments and can be propagated as estimates are scaled up (Larjavaara and Muller-Landau 2013). For example, the use of height–diameter (*H*–*D*) models, developed from the height and stem diameter of individual trees, often exhibit uncertainty due to wider height-variation at different spatial scales (Feldpausch *et al* 2011, Vieilledent *et al* 2012). Space-borne and air-borne LiDAR and RADAR technologies can improve the accuracy of the height measurement and have been used to develop canopy height models (Fatoyinbo *et al* 2021).

The Sundarbans mangrove forest is one of the largest and most bio-diverse mangroves in the world, located between Bangladesh and India. It contains the highest carbon densities (345 Mg ha^{-1}) in both above- and below-ground among all forests in Bangladesh (GOB 2019, Henry *et al* 2021). The Bangladesh Forest Department estimated carbon stocks in the Sundarbans in 2009 and 2015 using pan-tropical allometric models and Sundarbans-specific generic models (BFD 2010, Rahman *et al* 2015, Mahmood *et al* 2019, Henry *et al* 2021). Other studies such as Kamruzzaman *et al* (2017) and Azad *et al* (2020) used pan-tropical generic models to estimate AGB in selected areas. However, species-specific allometric models are not yet available to estimate AGB in the Sundarbans. Therefore, it is timely to examine whether species-specific allometric models using measured wood densities and tree heights can yield more accurate estimates of AGB in the Sundarbans and in mangrove forests more generally. The aim of this paper is to report research that compares a range of sources of uncertainty in allometric models, WD, and height measurement for AGB in the Sundarbans mangrove forest, Bangladesh. First, the study compares site- and species-specific AGB between the Sundarbans and pan-tropical generic allometric models for variability of aboveground tree biomass. Secondly, the study determines variability of AGB in the Sundarbans by comparing measured and published WD values at multiple spatial scales. Thirdly, the study quantifies the impact of different methods of tree height determination on estimates of AGB in mangrove forests.

2. Material and methods

2.1. Study area

The Bangladesh Sundarbans is situated between 21°30′ N and 22°30′ N and 89°00′ E and 89°55′ E in the lower delta plain of the Ganges–Brahmaputra–Meghna delta covering an area of 6017 km^2 (figure 1) (Giri *et al* 2011, Aziz and Paul 2015, Sarker *et al* 2016). The forest is of international significance as a Ramsar and UNESCO World Heritage site. It provides a number of valuable ecosystem services such as protecting inland areas from storms and tidal surges (Barua *et al* 2020). The near-constant mean annual minimum and maximum temperature (29 °C–31 °C) and high annual rainfall (1474–2265 mm) made the climate of the Sundarbans warm and humid between 1948 and 2011 (Chowdhury *et al* 2016, Sarker *et al* 2016). The soil is fine-gained silt and clay and slightly calcareous (Siddiqi 2001). The Sundarbans has a distinct salinity zonation with the high salinity zone in the

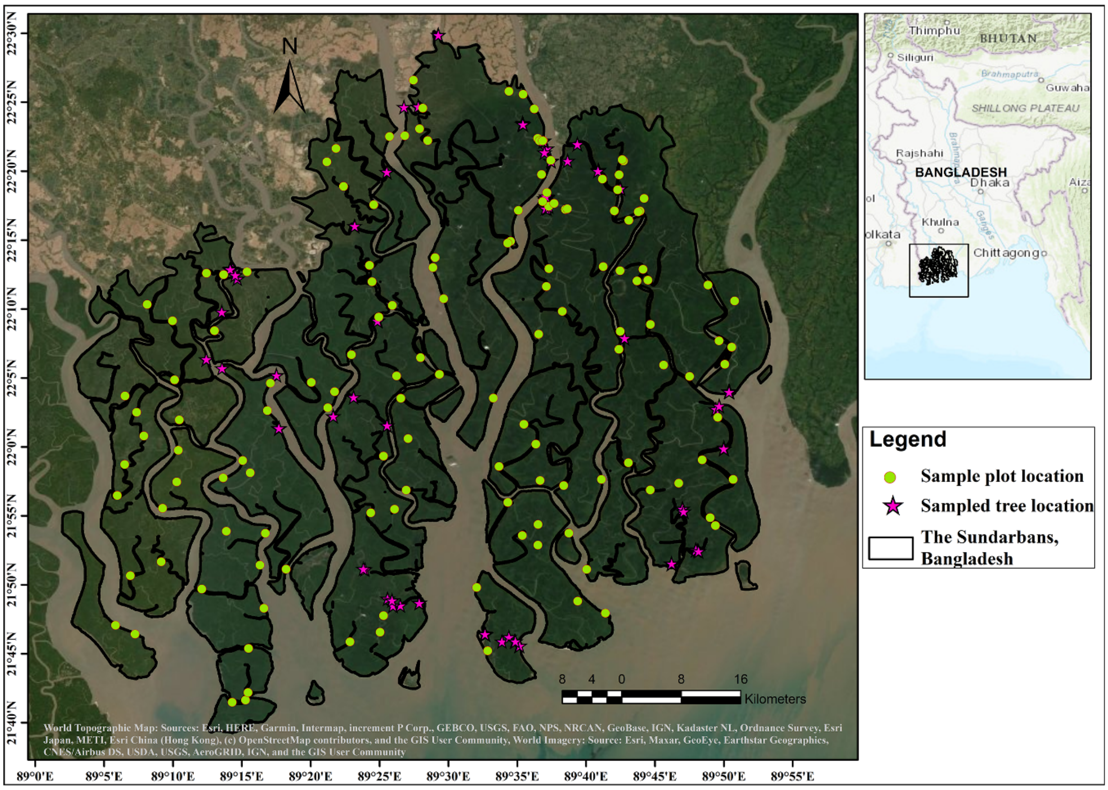

Figure 1. Sample plot location in the Sundarbans mangrove forest, Bangladesh. The pink star indicates tree location by Mahmood *et al* (2019).

west (polyhaline) to low salinity zone (oligohaline) in the east along with medium salinity zone (mesohaline) between (Siddiqi 2001, Chanda *et al* 2016). Salinity regulates the geomorphology and hydrological characteristics and also the morphology, growth and distribution of plant species (Sarker *et al* 2016, 2019a, Rahman *et al* 2020, 2021).

2.2. Allometric models in the Sundarbans

Species-specific allometric models are not available for all species in the Sundarbans as destructive sampling was not permitted due to an imposed felling moratorium of all species since 1989 (Mahmood *et al* 2019). However, four species-specific models were developed through destructive sampling in the Bangladesh Sundarbans (table 1). Three generic allometric models were recently developed for 14 species by using semi-destructive sampling methods where biomass of stems and larger branches were measured through volume and WD, and small branches and foliage through weighing after pruning (Mahmood *et al* 2019). Published pan-tropical models have also been used to estimate biomass in the Sundarbans (Rahman *et al* 2015, Kamruzzaman *et al* 2017, 2018).

2.3. Development of species-specific allometric model

A conceptual diagram of the research methodology is presented in the figure 2. The species-specific allometric models were developed from the semi-destructive sampling data (324 individuals, 13 species, except *Sonneratia caseolaris*) from Mahmood *et al* (2019), where AGB (kg/tree) was presented along with DBH and total height (H) (figure 1). Species-specific models for *S. caseolaris* were not developed as the independent tree inventory data did not have any individuals of this species. Out of 13 species, eight species (*Avicennia officinalis, Avicennia marina, Bruguiera gymnorrhiza, Bruguiera sexangula, Rhizophora apiculata, Rhizophora mucronata, Xylocarpus granatum* and *Xylocarpus moluccensis*) were merged into genus level to yield sufficient data for model fitting. Therefore, nine allometric models were developed for *Aglaia cucullata, Avicennia* sp., *Bruguiera* sp., *Excoecaria agallocha, Heritiera fomes, Lumnitzera racemosa, Rhizophora* sp., *Sonneratia apetala*, and *Xylocarpus* sp.

Log-linear ordinary least square regression was used to fit models to predict AGB for each species. The choice of log-linear regression over nonlinear regression was done by comparing error distribution of biomass. According to Xiao *et al* (2011), the linear regression of log-transformed data better characterizes multiplicative, heteroscedastic and lognormal error, whereas the nonlinear regression performs additive, homoscedastic, normal error. The goodness of fit of two models were compared and the lower value of Akaike's information criterion (AIC)

Table 1. Allometric models used for measuring aboveground biomass in the Sundarbans.

Model no.	Site, species	Allometric model	N	Identity in this paper and source
Bangladesh Sundarbans and species-specific				
1	*Aegialitis rotundifolia*	$AGB = 5.49GCH^2 - 251.36\ H - 0.07\ HCH + 0.75(GCH \times H \times HCH)$	29	Siddique *et al* (2012)
2	*Aegiceras corniculatum*	$\sqrt{AGB} = 0.48\ DBH - 0.13$	50	Mahmood *et al* (2016b)
3	*Ceriops decandra*	$AGB = 4.70\ GCH^{2.41}$	48	Mahmood *et al* (2012)
4	*Kandelia candel*	$AGB = 0.21\ DBH^2 + 0.12$	25	(Mahmood *et al* 2016a)
Bangladesh Sundarbans and generic model				
5	For 14 species *Aglaia cucullata,* *Avicennia officinalis,* *Avicennia marina,*	$\ln(AGB) = -1.9272 + 2.3517\ \ln(DBH)$	260	Mahmood_2019_D (Mahmood *et al* 2019)
6	*Bruguiera gymnorrhiza,* *Bruguiera sexangula,* *Excoecaria agallocha,* *Heritiera fomes,*	$\ln(AGB) = -2.4317 + 2.1341\ \ln(DBH) + 0.4953\ \ln(H)$	260	Mahmood_2019_DH (Mahmood *et al* 2019)
7	*Lumnitzera racemosa,* *Rhizophora apiculata,* *Rhizophora mucronata,* *Sonneratia apetala,* *Sonneratia caseolaris,* *Xylocarpus granatum,* *Xylocarpus moluccensis*	$\ln(AGB) = -6.7189 + 2.1634\ \ln(DBH) + 0.3752\ \ln(H) + 0.6895\ \ln(WD)$	260	Mahmood_2019_DHW (Mahmood *et al* 2019)
World or pantropical and generic model				
8	Pantropical, all species	$AGB = 0.0673 \times (WD \times DBH^2 \times H)^{0.976}$	4004	Chave_2014_DHW (Chave *et al* 2014)
9	Pan-tropical, mangrove species	$AGB = 0.0509 \times (WD \times DBH^2 \times H)$	84	Chave_2005_DHW (Chave *et al* 2005)
10	Pan-tropical, mangrove species	$AGB = WD \times \exp(-1.349 + 1.980\ \ln(DBH) + 0.207\ (\ln(DBH))^2 - 0.0281\ (\ln(DBH))^3)$	84	Chave_2005_DW (Chave *et al* 2005)
11	South-east Asia, mangrove species	$AGB = 0.251 \times WD \times DBH^{2.46}$	104	Komiyama_2005_DW (Komiyama *et al* 2005)

Here AGB = total above ground biomass (kg), N = number of destructive/semi-destructive samples, DBH = diameter at breast height (cm), H = total height (m), WD = wood density (gm cm^{-3}, model-7: kg m^{-3}), GCH = girth at collar height (cm), HCH = height of collar girth point (m).

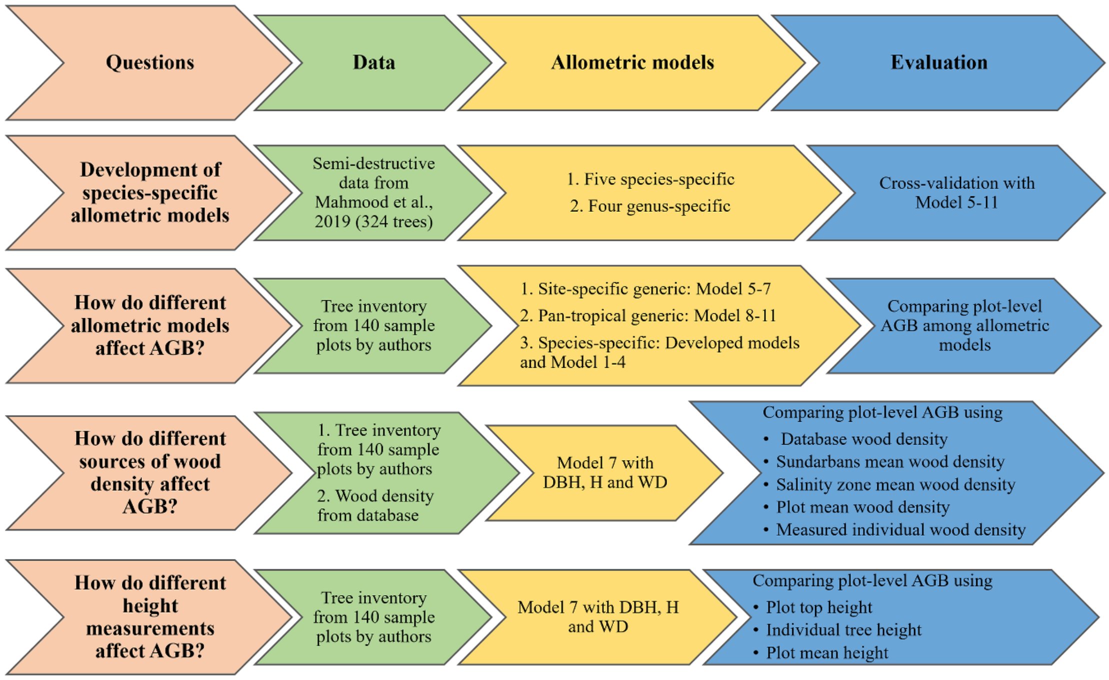

Figure 2. Conceptual diagram of the research methodology. The model numbers are labeled according to table 1. Here, DBH: diameter at breast height, H: height and WD: wood density.

provides significantly better fit when the magnitude of the difference of AIC is greater than 2 (Burnham and Anderson 2002). These two models were compared for all species following Xiao *et al* (2011). In all cases, the log-linear regression provided significantly better fit (table A.1 available online at stacks.iop.org/ERL/16/124002/mmedia). Therefore, the following six log-linear regression models were used to fit AGB as the dependent variable, and DBH and tree height (H) as independent variables

$$\text{E1: } \ln(\text{AGB}) = \ln(a) + b\ln(\text{DBH})$$
$$\text{E2: } \ln(\text{AGB}) = \ln(a) + b\ln(\text{H})$$
$$\text{E3: } \ln(\text{AGB}) = \ln(a) + b\ln(\text{DBH} \times \text{H})$$
$$\text{E4: } \ln(\text{AGB}) = \ln(a) + b\ln(\text{DBH}^2 \times \text{H})$$
$$\text{E5: } \ln(\text{AGB}) = \ln(a) + b\ln(\text{DBH} \times \text{H}^2)$$
$$\text{E6: } \ln(\text{AGB}) = \ln(a) + b\ln(\text{DBH}) + c\ln(\text{H}).$$

The underlying assumptions for the regression analysis such as normality of residuals and heteroscedasticity were used to judge the suitability of each regression model. Percent relative standard errors (PRSEs) of each regression coefficient was measured according to Sileshi (2014), where PRSE > 25 is considered an unreliable model. The multicollinearity of each model was measured with the variance inflation factor (VIF), where VIF > 5 indicates high collinearity among independent variables. Due to high multicollinearity, complex models with more independent variables were not considered in this study. After obtaining the eligible potential models for each species, the best models were selected by the lowest second-order Akaike information criterion (AICc) and residual standard error (RSE), and the highest Akaike information criterion weight (AICw) and coefficient of determination (R^2) values (Picard *et al* 2012, Sileshi 2014, Mahmood *et al* 2019, 2020). Models with non-significant parameter of estimates were not considered regardless of meeting the criteria outlined. Since, the AICw provides the likelihood of each model to be the best, it was given highest priority compared with other parameters (Sileshi 2014). For all models, the correction factor was calculated to minimize systematic bias while converting biomass from ln scale to normal scale (Sprugel 1983). The K-fold cross-validation technique was used to validate the best model. This technique randomly divides the original dataset into K subsets (ten in this case) of equal sizes, where each subset is validated with $K - 1$ subsets (James *et al* 2013). The K-fold validation technique was also run for Sundarbans-specific and pantropical generic model (Model no. 7–11 in table 1) to measure tree level variability in AGB in the Sundarbans.

2.4. Tree inventory

Aboveground tree data were collected from 140 random sample plots within the Bangladesh Sundarbans (figure 1). Out of 140 sample plots, 120 plots were randomly placed within permanent sample plot (PSP) (20 × 100 m) established by the Bangladesh Forest Department whilst the remaining 20 plots were outside of the PSP. These sample plots are distributed to all 55 compartments in the Bangladesh Sundarbans covering all three salinity zones (oligohaline, mesohaline and polyhaline) and forest types (Iftekhar and

Saenger 2008, Sarker *et al* 2019b). Each plot consists of a circular plot with the radius of 11.3 m (400 m^2) for measuring bigger trees (DBH > 14.5 cm) and a smaller circular plot within this of 5 m radius (79 m^2) for smaller trees (DBH > 2.5–14.5 cm) (figure A.1). After establishing the plots, all individual trees (DBH > 2.5 cm) were marked, and DBH and total height (H) measured by using a diameter tape and a Vertex III hypsometer (Haglöf, Sweden), respectively. Haglöf wood increment borer (5.15 mm diameter and 300 mm bit length) was used to collect woody specimen at DBH point to determine the WD of studied species according to Wiemann and Williamson (2013). The WD (gm cm^{-3}) was then measured from the volume and dry mass of the specimen. The cylindrical volume was measured in the field from the diameter and length of the specimen and brought to the laboratory for oven-drying at 105 °C until constant weight.

2.5. Variability of AGB in the Sundarbans

The magnitude and patterns of differences in AGB at plot level in the Sundarbans were compared by using different allometric models with an independent set of collected inventory data from the Sundarbans. Plot level AGB variability was measured by actual AGB difference (Mg ha^{-1}), absolute difference (Mg ha^{-1}) and relative absolute difference (%) among different allometric models.

2.5.1. AGB variability with allometric models

Measured DBH, H and WD were used in the species-specific allometric models and other site-specific and pan-tropical generic models (Model 7–11 in table 1) to assess AGB at the individual tree level. In order to compute plot-level AGB estimation per hectare (Mg ha^{-1}), a hectare expansion factor (HEF) for each stem was used according to the size of the sample plot (i.e. HEF = 25 for bigger plots, and HEF = 126.58 for smaller sub-plot) and subsequently summed up all tree biomass in each plot to get plot biomass. To estimate biomass from the species-specific models, the developed nine species-specific models were used alongside four published species-specific models (Model 1–4 in table 1). If no species-specific allometric model was available, models for similar genus or family level were applied. Since measuring the girth at collar height (GCH) for *Ceriops decandra* and *Aegialitis rotundifolia* is laborious and time consuming, DBH was measured in the field and subsequently converted to GCH from the developed relationship between DBH and GCH of 50 individuals (figure A.2).

2.5.2. AGB variability with WD

Variation of tree AGB was compared with measured and databases-sourced WD obtained from published WD databases including the global WD database (Chave *et al* 2009, Zanne *et al* 2009), World Agroforestry's tree functional attributes and ecological databases (ICRAF 2016) and from Bangladesh Forest Research Institute (Sattar *et al* 1995). The Sundarbans-specific generic allometric model (Model 7: Mahmood_2019_DHW) was used for comparison of AGB from multiple WD sources. If there was no measured WD for any species, the WD from the same genus or family was used. Instead of applying species WD, plot-level mean WD, salinity zone WD and Sundarbans level WD were used to investigate how the spatial scale of WD variation on AGB estimates in the Sundarbans. To measure salinity zone mean WD, measured WD were averaged according to three salinity zones in the Sundarbans according to Rahman *et al* (2021).

2.5.3. AGB variability with tree height

To derive the variation of AGB from different height measurement, mean height and maximum height from each plot was used in Model 7 (Mahmood_2019_DHW). The Model 7 was used in this case as it is originated from the Sundarbans and it contains both H and WD parameters.

2.6. Statistical analysis

All statistical analysis and graphics used R4.0.4 for Windows in RStudio Version-1.4.1106 (R Core Team 2020). The normality of residuals, heteroscedasticity and multicollinearity of each regression model were tested with Shapiro–Wilk normality test by using 'R stats' base package, studentized Breusch–Pagan test by using 'lmtest' package and VIF test using 'car' package, respectively (Zeileis and Hothorn 2002, Fox and Weisberg 2019). AICc for fitted regression model was assessed by 'MuMIn' package (Bartoń 2020). *K*-fold cross validation was run using 'caret' package and model accuracy was compared with mean absolute error (MAE) and root mean squared error (Kuhn 2008). Pairwise comparison of tree AGB between the species-specific and other models were tested either by paired *t*-test if the underlying assumptions such as normality and heteroscedasticity were met; otherwise, Wilcoxon signed-rank non-parametric test was used. The 'rstatix' package was used for Wilcoxon signed-rant test and 'R stats' base package was used for paired *t*-test (Kassambara 2020). The graphical output was generated using the 'ggplot2' 'ggeffects' and 'cowplot' package (Wickham 2016, Lüdecke 2018, Wilke *et al* 2019).

3. Results

3.1. Species-specific allometric model

Out of 54 log-linear regression models for nine species, 26 models passed all four criteria including normality of residuals, heteroscedasticity, PRSE and VIF (table A.2). These 26 models were then fitted species-wise to the 324 semi-destructively harvested tree dataset with DBH and H: *A. cucullata* (19),

Table 2. Regression results for all species-specific allometric models in the Sundarbans.

Species	Eq. no.	Model, ln (AGB) =	a^*	b	c	Adj. R^2	RSE	AICc	AICw	CF
Aglaia cucullata	**E1**	$\mathbf{ln(a) + b\,ln\,(DBH)}$	−1.9066	2.3784	—	0.9915	0.1047	−26.3501	1.00	1.0055
	E5	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H}^2)$	3.7114	1.0918	—	0.9585	0.2316	3.8164	0.00	1.0980
	E2	$\ln(a) + b \ln(\mathrm{H})$	4.5892	3.7109	—	0.8554	0.4324	27.5502	0.00	1.0272
Avicennia sp.	**E1**	$\mathbf{ln(a) + b\,ln\,(DBH)}$	−1.5554	2.2069	—	0.9781	0.2287	0.0103	0.81	1.0265
	E4	$\ln(a) + b \ln(\mathrm{DBH}^2 \times \mathrm{H})$	−2.7625	0.9520	—	0.9765	0.237	2.8854	0.19	1.0285
Bruguiera sp.	**E1**	$\mathbf{ln(a) + b\,ln\,(DBH)}$	−1.4473	2.2870	—	0.9845	0.1926	−9.3234	1.00	1.0187
	E3	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H})$	−2.7982	1.5246	—	0.9649	0.2901	16.0743	0.00	1.0430
	E5	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H}^2)$	−3.1823	1.1004	—	0.9178	0.4439	42.4386	0.00	1.1035
Excoecaria agallocha	**E4**	$\mathbf{ln(a) + b\,ln\,(DBH^2 \times H)}$	−2.5721	0.8623	—	0.9903	0.1539	−26.9780	1.00	1.0119
	E3	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H})$	−2.9335	1.4173	—	0.9801	0.2200	−1.9475	0.00	1.0245
	E5	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H}^2)$	−3.3198	1.0359	—	0.9591	0.3152	50.1953	0.00	1.0509
	E2	$\ln(a) + b \ln(\mathrm{H})$	−4.0227	3.6582	—	0.8558	0.5919	67.3342	0.00	1.1915
Heritiera fomes	**E1**	$\mathbf{ln(a) + b\,ln\,(DBH)}$	−1.9944	2.4603	—	0.9931	0.1434	−97.2721	1.00	1.0103
Lumnitzera racemosa	**E1**	$\mathbf{ln(a) + b\,ln\,(DBH)}$	−2.1151	2.4187	—	0.9858	0.1342	−8.8255	0.94	1.0090
	E4	$\ln(a) + b \ln(\mathrm{DBH}^2 \times \mathrm{H})$	−3.2562	1.0631	—	0.9783	0.1663	−3.2570	0.06	1.0139
	E3	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H})$	−4.0458	1.8671	—	0.9558	0.2373	5.9931	0.00	1.0286
	E5	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H}^2)$	−4.9734	1.4650	—	0.8994	0.3579	16.6722	0.00	1.0661
Rhizophora sp.	**E4**	$\mathbf{ln(a) + b\,ln\,(DBH^2 \times H)}$	−2.3744	0.8953	—	0.9467	0.2226	2.8788	0.82	1.0251
	E3	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H})$	−2.8960	1.5009	—	0.9358	0.2443	6.0407	0.17	1.0303
	E5	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H}^2)$	−3.4321	1.1161	—	0.9065	0.2948	12.4334	0.01	1.0444
Sonneratia apetala	**E4**	$\mathbf{ln(a) + b\,ln\,(DBH^2 \times H)}$	−2.8869	0.9170	—	0.9938	0.1633	−10.3304	0.71	1.0134
	E6	$\ln(a) + b \ln(\mathrm{DBH}) + c \ln(\mathrm{H})$	−2.6715	1.9068	0.7430	0.9939	0.1625	−8.5123	0.29	1.0133
	E3	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H})$	−3.6314	1.5533	—	0.9854	0.2518	6.9904	0.00	1.0322
	E5	$\ln(a) + b \ln(\mathrm{DBH} \times \mathrm{H}^2)$	−4.4509	1.1706	—	0.9582	0.4256	27.9819	0.00	1.0948
	E2	$\ln(a) + b \ln(\mathrm{H})$	−5.6705	4.2261	—	0.7723	0.9932	61.8759	0.00	1.6375
Xylocarpus sp.	**E1**	$\mathbf{ln(a) + b\,ln\,(DBH)}$	−1.9174	2.3100	—	0.9720	0.1989	−15.5152	1.00	1.0200

Here bold and light grey shaded models are the best model for each species, a^* stands for ln (a), all parameters of estimates (a, b and c) are significant at $p < 0.05$. R^2: coefficient of determination, RSE: residual standard error, AICc: with small sample bias adjustment, AICw: weighted AIC, CF = correction factor for converting log scale in to normal scale.

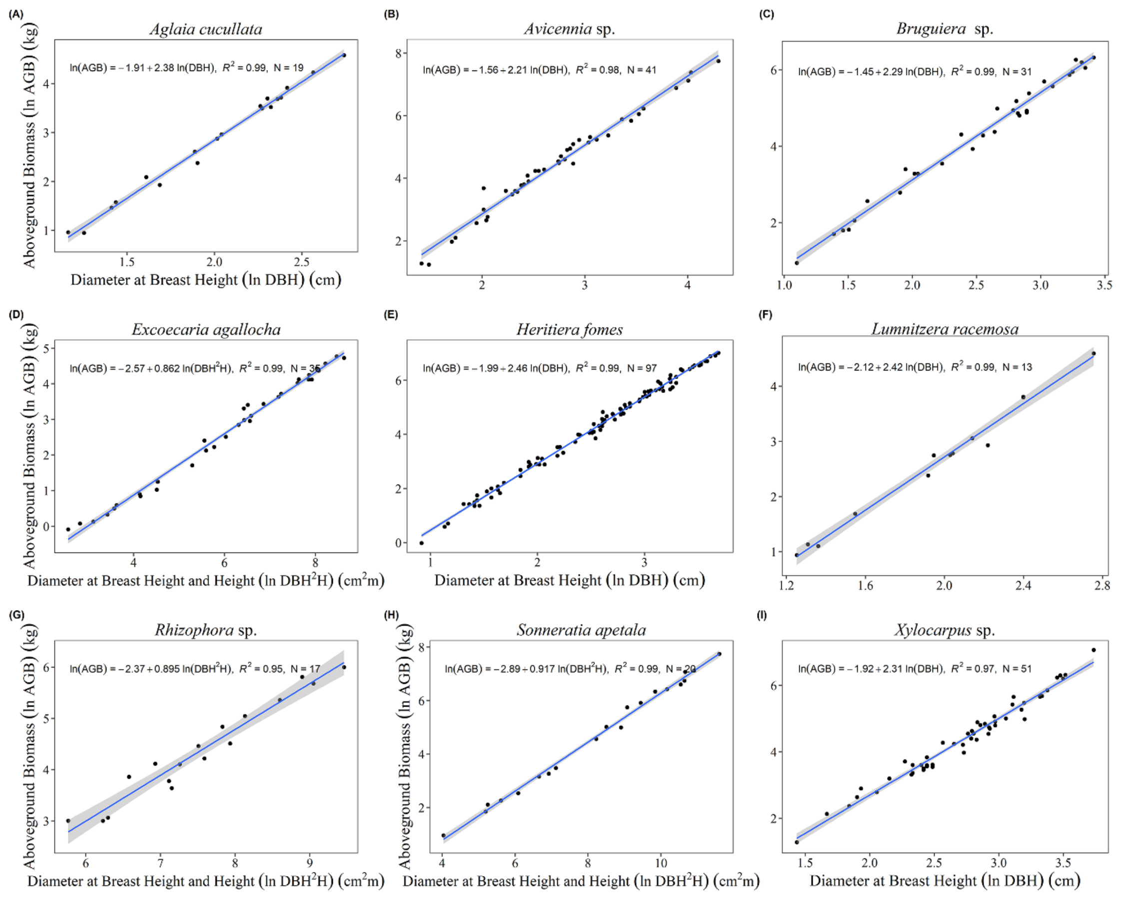

Figure 3. Best species-specific allometric model aboveground biomass in the Sundarbans.

Avicennia sp. (41), *Bruguiera* sp. (31), *E. agallocha* (35), *H. fomes* (97), *L. racemosa* (13), *Rhizophora* sp. (17), *S. apetala* (20), and *Xylocarpus* sp. (51).

Out of 26 models, the best nine species-specific models are presented for each species group (table 2; figure 3). The AICw shows that the best-chosen models for *A. cucullata*, *Bruguiera* sp., *E. agallocha*, *H. fomes*, and *Xylocarpus* sp. have 100% chance for being the best model, while *Avicennia* sp., *L. racemosa*, *Rhizophora* sp. and *S. apetala* have respectively 81%, 94%, 82%, and 71% chance to be the best model (table 3). In the case of *S. apetala*, while E6 models had the highest and lowest RSE and AIC value, the E4 model was chosen based on higher AICw for its greater chance for being the best model. The adjusted coefficient of determination (R^2) varied from 0.77 to 0.99 for all models. All species-specific models comprised single predictor value with only DBH for six species: *A. cucullata*, *Avicennia* sp., *Bruguiera* sp., *H. fomes*, *L. racemosa*, and *Xylocarpus* sp. and with combination of DBH and H ($DBH^2 \times H$) for *E. agallocha*, *S. apetala*, and *Rhizophora* sp.

The ten-fold cross validation showed that the species-specific model gives the lowest average MAE of all species in comparison to three Sundarbans-specific and four pan-tropical generic allometric models (figure 4, table A.4). The lowest average MAE revealed that the species-specific models performed well to predict the AGB in the Sundarbans. AGB estimation at tree level had mean relative absolute difference in MAE between 21.85% with Mahmood_2019_DHW model to the maximum 167.43% with Komiyama_2005_DW model followed by Chave_2005_DHW and Chave_2014_DHW (table A.4). The paired *t*-test of MAE for species-specific models with generic models showed that there is no significant difference of MAE with three Sundarbans-specific models ($p > 0.05$); however, all four pan-tropical models showed significantly higher MAE than the species specific-model ($p < 0.05$). The largest error was obtained for *E. agallocha* with Komiyama_2005_DW.

3.2. Aboveground tree biomass in the Sundarbans

The tree inventory in the Bangladesh Sundarbans indicates a total of 24 tree species. The mean DBH, height, measured and database-sourced WD of all tree species are presented in the table 3. The DBH and H distribution are presented in the supplementary figures A.3 and A.4. Frequency distribution of the topmost ten species based on basal area ($m^2\ ha^{-1}$) and tree density ($trees\ ha^{-1}$) showed that *E. agallocha*, *H. fomes* and *C. decandra* comprise 90% of the stems in the Sundarbans, although they represent 60% in

Table 3. List of tree species found in the Sundarbans with taxonomy and structural parameters.

Sl No.	Latin name	Local name	Family	Mean DBH (cm ± s.d.)	Mean height (m ± s.d.)	Measured mean wood density (gm cm^{-3} ± s.d.)	Mean wood density from database (gm cm^{-3} ± s.d.)[b]
1.	*Aegialitis rotundifolia* Roxb.	Nunia	*Plumbaginaceae*	6.86 (±2.85)	3.94 (±1.71)	—	0.50 (±0.05)
2.	*Aegiceras corniculatum* (L.) Blanco	Kholshi	*Primulaceae*	5.69 (±2.67)	5.73 (±2.18)	0.74	0.60 (±0.08)
3.	*Aglaia cucullata* (Roxb.) Pellegr.[a]	Amur	*Meliace*	3.58 (±1.16)	4.70 (±1.62)	0.50	0.62 (±0.12)
4.	*Avicennia alba* Blume.	Sada Baen	*Avicenniaceae*	14.10 (±0.85)	8.70 (±2.40)	0.72 (±0.08)	0.70 (±0.12)
5.	*Avicennia marina* (Forssk.) Vierh.	Moricha Baen	*Avicenniaceae*	10.40 (±5.26)	10.87 (±5.77)	0.55	0.64 (±0.09)
6.	*Avicennia officinalis* L.	Kala Baen	*Avicenniaceae*	21.20 (±13.40)	11.56 (±5.13)	0.61 (±0.07)	0.65 (±0.08)
7.	*Bruguiera gymnorrhiza* (L.) Lam.	Lal Kakra	*Rhizophoraceae*	7.40	5.80	—	0.76 (±0.08)
8.	*Bruguiera sexangula* (Lour.) Poir.	Holud Kakra	*Rhizophoraceae*	15.75 (±3.95)	6.96 (±3.02)	0.69 (±0.03)	0.83 (±0.12)
9.	*Cerbera manghas* L.[a]	Dakur	*Apocynaceae*	8.92 (±0.08)	0.72 (±0.08)	0.35 (±0.01)	0.47 (±0.05)
10.	*Ceriops decandra* (Griff.) Ding Hou	Goran	*Rhizophoraceae*	3.31 (±0.80)	3.97 (±0.95)	0.73 (±0.07)	0.73 (±0.25)
11.	*Cynometra ramiflora* L.[a]	Singra	*Fabaceae*	4.25 (±1.55)	5.05 (±1.47)	0.66 (±0.05)	0.84 (±0.10)
12.	*Excoecaria agallocha* L.	Gewa	*Euphorbiaceae*	6.93 (±4.04)	6.71 (±2.49)	0.42 (±0.08)	0.43 (±0.06)
13.	*Excoecaria indica* (Willd.) Muell. Arg.[a]	Batul	*Euphorbiaceae*	6.60	6.80	0.41	0.50 (±0.02)
14.	*Heritiera fomes* Buch.-Ham.	Sundri	*Malvaceae*	8.57 (±6.58)	8.03 (±4.16)	0.75 (±0.07)	0.88 (±0.11)
15.	*Hibiscus tiliaceus* L.[a]	Bola	*Malvaceae*	3.90	5.00	—	0.48 (±0.06)
16.	*Intsia bijuga* (Colebr.) Kuntze[a]	Bhaila/Bhola	*Fabaceae*	4.40 (±0.79)	5.17 (±0.81)	—	0.71 (±0.20)
17.	*Kandelia candel* (L.) Druce	Vatkathi	*Rhizophoraceae*	11.87 (±5.09)	7.77 (±1.15)	0.58 (±0.05)	0.52 (±0.05)
18.	*Lumnitzera racemosa* Willd.	Kirpa	*Combretaceae*	5.23 (±1.84)	5.99 (±1.13)	0.82 (±0.13)	0.83 (±0.08)
19.	*Millettia pinnata* (L.) Panigrahi[a]	Karanj	*Fabaceae*	5.70	6.30	0.55	0.61 (±0.05)
20.	*Rhizophora apiculata* Blume.	Bhora Jhana	*Rhizophoraceae*	13.54	0.72	—	0.88 (±0.21)
21.	*Rhizophora mucronata* Lamk.	Jhana Garjan	*Rhizophoraceae*	15.42 (±3.72)	10.38 (±2.65)	0.95 (±0.05)	0.85 (±0.10)
22.	*Sonneratia apetala* Buch.-Ham.	Keora	*Lythraceae*	29.35 (±12.84)	17.97 (±5.90)	0.54 (±0.07)	0.53 (±0.11)
23.	*Xylocarpus granatum* K.D. Koen.	Dhundul	*Meliaceae*	18.77 (±12.03)	8.08 (±2.66)	0.58 (±0.05)	0.67 (±0.14)
24.	*Xylocarpus moluccensis* (Lam.) M. Roem	Passur	*Meliaceae*	15.51 (±10.80)	9.39 (±3.95)	0.65 (±0.09)	0.65 (±0.09)

[a] Indicates mangrove associates according to Tomlinson (2016). Abbreviation: DBH = diameter at breast height. Values without s.d. indicates single observation.

[b] Multiple wood density values from different sources.

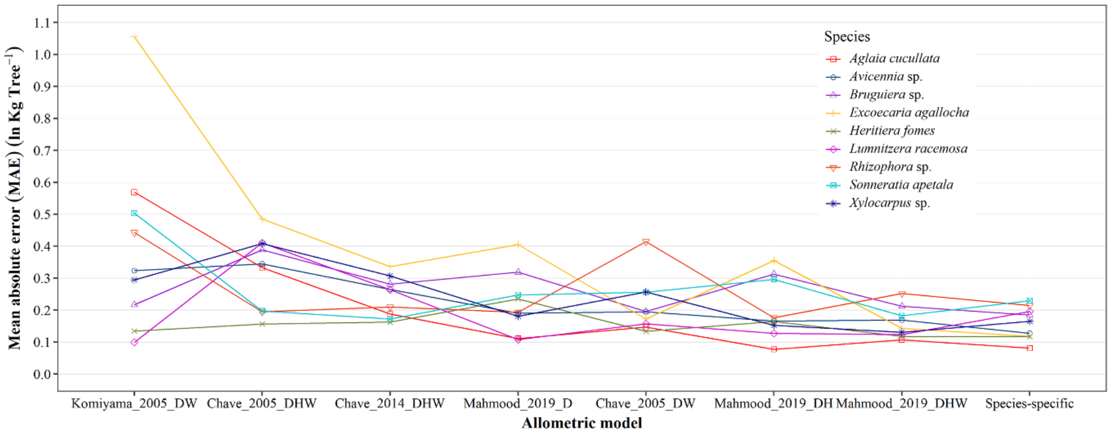

Figure 4. Species-wise mean absolute error (MAE) of tree AGB with all allometric models after ten-fold cross validation. The models are arranged from highest average MAE to minimum.

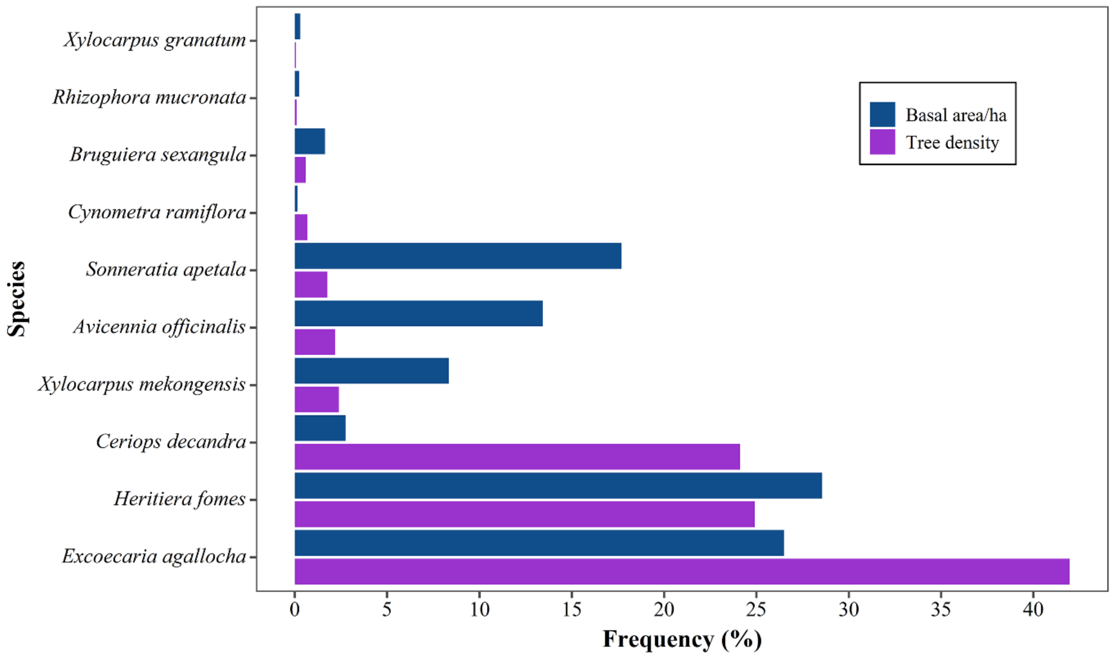

Figure 5. Frequency distribution of the ten most frequently occurring species based on basal area (m^2 ha^{-1}) and tree density (tree ha^{-1}).

terms of basal area (figure 5). *E. agallocha* and *H. fomes* was within the top two species in both categories; *C. decandra* was the third in terms of tree density, however, the sixth in case of basal area for its lower DBH.

The mean AGB varied from 111.36 Mg ha^{-1} with the Chave_2005_DHW model to the highest 299.48 Mg ha^{-1} for Chave_2005_DW model (figure 6). Except for Chave_2005_DHW and Chave_2014_DHW, all other models yielded higher AGB than the species-specific model (123 Mg ha^{-1}). The mean relative absolute difference in AGB ranged from 9% with Mahmood_2019_DHW to 142% with Chave_2005_DW. Pairwise comparison with the Wilcoxon signed-rank test between species-specific and other models showed that all generic models measured significantly different AGB than the species-specific model in the Sundarbans ($p < 0.05$). Both Chave_2005_DW and Komiyama_2005_DW overestimated AGB (supplementary table A.5). The absolute difference between allometric models tended to increase with DBH in all species, suggesting that larger trees are crucial for estimating AGB with a variety of available allometric model leading to a greater error and uncertainty.

AGB was significantly higher when models used published WD compared to species-specific measured WD (Wilcoxon signed-rank test, $p < 0.05$) (figure 7(A), table 4). The maximum mean relative difference biomass was for Sundarbans mean WD

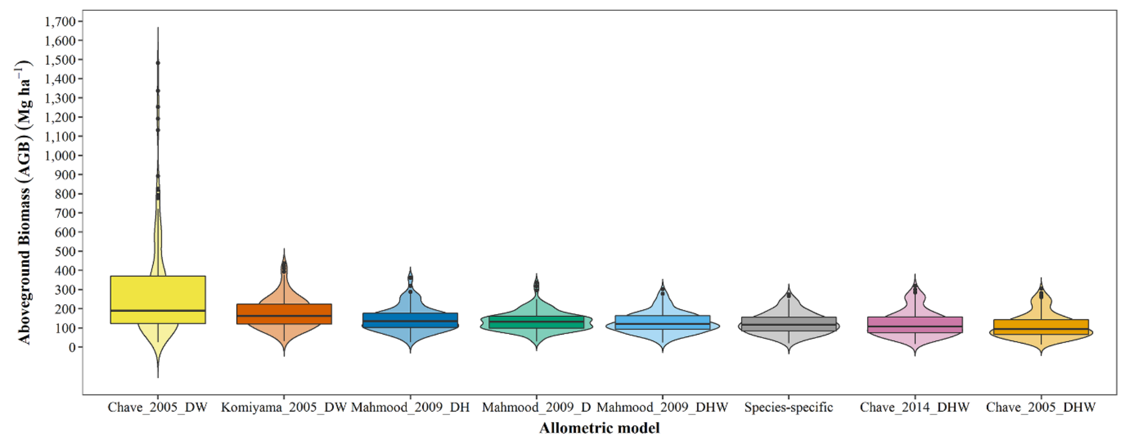

Figure 6. Comparison of aboveground biomass (Mg ha^{-1}) with different allometric models. The models are arranged from the highest median AGB to the lowest. The black horizontal line of box plot for each model represents the median and the width of violin plot represents the proportion of the data located there as a measure of kernel probability density. The black dots represent the outliers, which are 1.5 times of the interquartile range above the upper quartile and below the lower quartile (McGill *et al* 1978).

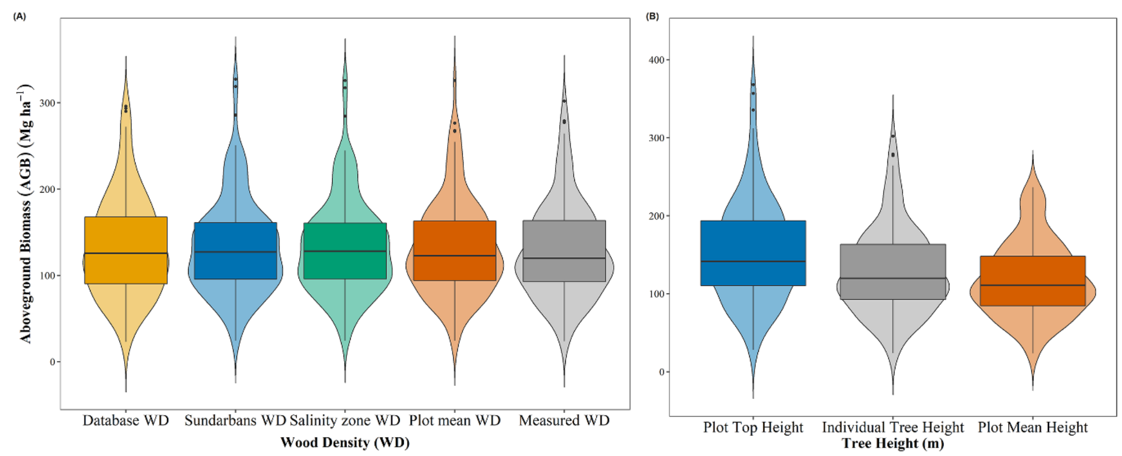

Figure 7. Comparison of aboveground biomass with (A) different wood density and (B) different height parameters. The parameters are arranged from the highest median AGB to the lowest. For details of the violin-box plot, see figure 6.

followed by salinity zone mean WD and database-derived WD. Looking at different sources of height data, using plot top height tended to be overestimate AGB by 19.46%, while using average height underestimated AGB by 8.31% compared to the measurements from individual species (figure 7(B), table 4).

4. Discussion

The results show that the species-specific allometric models provide the lowest average MAE for all species in the Sundarbans (figure 4, table A.4). However, the three Sundarbans-specific generic models showed no significant difference of mean MAE at tree-level compared with the species-specific models (table A.4). At plot-level, all local and pan-tropical generic models either overestimated or underestimated AGB when compared to local species-specific models (figure 6). Several studies have concluded that site-specific AGB models estimate biomass or carbon with less error than regional or pan-tropical models; for example, Sundarbans mangrove forest (Mahmood *et al* 2019), lowland Dipterocarp forest in Indonesia (Basuki *et al* 2009), degraded landscape in Northern Ethiopia (Mokria *et al* 2018), central African forest (Ngomanda *et al* 2014) and Mexican tropical humid forests (Martínez-Sánchez *et al* 2020). In contrast, only a few studies report better performance from regional or pan-tropical models and these appear result from large uncertainties in the data used to build the local model; for example, West Africa (Aabeyir *et al* 2020). The accuracy of these generic models for a particular forest depends on whether these models incorporate sufficient samples from that forest. Chave *et al* (2014) point out that the discrepancy between local models and their own model (Chave_2014_DHW) in wet forests (including mangroves) is largely due to failure to address the wider variation of tree form and other characteristics like

Table 4. Pairwise comparison test of plot-level AGB from species-specific and other allometric models.

Model comparison	Mean difference biomass (Mg ha^{-1})	Mean absolute difference biomass (Mg ha^{-1})	Mean relative absolute difference (%)	Wilcoxon signed-rank test (Z), p-value
Comparison of different allometric model				
Species-specific—Mahmood_2019_DHW	−5.18	11.38	9.21	$Z = -5.13$, $p < 0.05$
Species-specific—Chave_2014_DHW	0.79	17.38	14.07	$Z = -2.89$, $p < 0.05$
Species-specific—Mahmood_2019_D	−12.66	19.66	15.92	$Z = -6.40$, $p < 0.05$
Species-specific—Chave_2005_DHW	12.59	21.07	17.06	$Z = -6.51$, $p < 0.05$
Species-specific—Mahmood_2019_DH	−21.27	23.37	18.92	$Z = -7.95$, $p < 0.05$
Species-specific—Komiyama_2005_DW	−52.47	52.57	42.57	$Z = -10.26$, $p < 0.05$
Species-specific—Chave_2005_DW	−175.67	175.75	142.31	$Z = -10.26$, $p < 0.05$
Comparison from different wood density (WD)				
Measured WD—plot mean WD	−3.16	5.83	4.53	$Z = -5.86$, $p < 0.05$
Measured WD—database WD	−4.82	9.91	7.70	$Z = -3.83$, $p < 0.05$
Measured WD—salinity zone mean WD	−4.08	12.46	9.68	$Z = -3.54$, $p < 0.05$
Measured WD—Sundarbans mean WD	−4.29	12.47	9.69	$Z = -3.59$, $p < 0.05$
Comparison from different Tree Height (m)				
Individual height—plot mean height	10.70	10.70	8.31	$Z = -13.68$, $p < 0.05$
Individual height—plot top height	−25.04	25.04	19.46	$Z = -13.68$, $p < 0.05$

buttresses, which are common in the Sundarbans. Their previous model (Chave_2005_DW) overestimated AGB in the Sundarbans because of its inability to estimate biomass from larger trees (DBH > 42 cm) (Chave *et al* 2005). However, surprisingly, the worldwide generic models for mangroves also overestimate AGB, possibly because of the samples drawn from the mangroves of Asia-Pacific and Australia (Komiyama *et al* 2008).

The structure and morphological characteristics of all mangroves vary according to their ability to adapt to environmental conditions such as salinity, which is less pronounced in other wet and dry tropical areas (Ball and Pidsley 1995, Tomlinson 2016). Environmental drivers such as salinity and water deficit are considered the main stressors for the growth and development of mangroves, including the Sundarbans. For example, the third most abundant species in the Sundarbans, *C. decandra*, is a multi-stemmed bushy species, on the other hand, the top two, *H. fomes* and *E. agallocha* are tree-like structures. The pantropical models yielded a large error in the dwarf, bushy species and other true mangrove species in the Sundarbans (table A.5). Moreover, the extreme salinity has reduced the stature (Rahman *et al* 2015), trunk diameter (Rahman *et al* 2020) and the leaf area (Khan *et al* 2020) of *H. fomes* and *S. apetala*, present in all three salinity zones in the Sundarbans. Due to these wider morphological variation, Banerjee *et al* (2013) highlighted the importance of developing models based on salinity zonation.

This study demonstrates that when using measured wood densities and individual tree heights, generic equations yield accurate estimates of AGB in mangroves at the plot scale (figure 7). Most species had a higher published WD than the measured value seen in table 3 (Henry *et al* 2010). The use of WD from different databases such as the Global WD database resulted in a 9% variation for species having multiple values, which could provide a significant variation in AGB if upscaled (Réjou-Méchain *et al* 2019). Averaging WD at the plot scale, salinity zone scale or ecosystem scale also introduces errors. While WD is considered an important variable to capture a range of characteristics such as high density versus low density timber species, climax versus pioneer species or primary versus secondary species, the use of WD value from the secondary sources or averaging them in the higher scales might not reflect the true biomass (Slik *et al* 2008, Kenzo *et al* 2009). Phillips *et al* (2019) noted significant AGB error in the Amazon rainforest while scaling up from the plot level to forest and amazon-wide level. Yuen *et al* (2016) observed 31 Mg ha^{-1} higher AGB with the difference of measured and published WD of only 0.13 gm cm^{-3}.

Among nine developed models, six models showed that DBH alone is a strong predictor of AGB across the Bangladesh Sundarbans. The remaining three models of *E. agallocha, S. apetala*, and *Rhizophora* sp. showed sensitivity to height. However, the inclusion of top height or average height instead of using individual tree height can increase the error at the plot level and above. Kearsley *et al* (2013) observed 24% overestimation of AGB in the central Congo Basin by using a regional height–diameter relationship developed by Feldpausch *et al* (2012) compared to the local relationship. On the other hand, using mean height could reduce the difficulty of taking height measurements in dense forests, yet may lead to a significant underestimation of AGB (Hunter *et al* 2013). The difficulty of measuring height under a dense forest canopy allows researchers to use H-D relationship or to use bioclimatic variables in allometric models. However, these also lead to non-uniform bias in biomass estimation (Réjou-Méchain *et al* 2019).

Although species-specific WD and individual height data can be used to accurately estimate AGB at the plot and ecosystem level, collecting species information is impractical in highly diverse mixed tropical forests such as in Amazonia, Southeast Asia and the Congo basin, which comprise of more than 53 000 tree species (Feldpausch *et al* 2012, Slik *et al* 2015). Mangroves, by comparison exhibit less diversity. Developing allometric models for dominant species could improve the biomass inventory. For example, in the Sundarbans only 28 species were recorded (24 in this survey) and just three species (*E. agallocha, H. fomes* and *C. decandra*) constitute about 90% of stand density (figure 5), which implies that developing three allometric models is enough to produce acceptable AGB estimates in the Sundarbans (GOB 2019). The model used for *C. decandra* was developed by destructive sampling from Hossain *et al* (2012) and so this study recommends developing models with destructive samples from all salinity zones for *H. fomes* and *E. agallocha*.

The errors and uncertainties in the individual tree and plot level AGB estimates will result in large errors when scaling up to the ecosystem, region or country level by RS techniques. Réjou-Méchain *et al* (2019) described the errors due to poor choice of allometric models and failure to capture variabilities of WD and H as uniform and non-uniform bias. Uniform bias systematically propagates over- or underestimation whereas non-uniform bias is related to an inability to capture the variabilities across landscapes, for example, WD and H variation among successional stages or environmental gradients such as the salinity in the Sundarbans (Rahman *et al* 2020). These two types of bias, in addition to mapping errors resulting from the use of RS, may result in serious anomalies in national and global carbon budgets and result in poor understanding of species contribution to ecosystem processes and function in mangroves.

5. Conclusion

This study developed and tested five species-specific and four genus-specific allometric models for the nine most important species in the Sundarbans. All developed models explained a high percentage of the variance in tree AGB ($R^2 = 0.97$–0.99) using measured DBH and total height (H) data. At the individual tree level, the generic allometric models overestimated AGB between 22% and 167% compared to the species-specific models and at the plot level, they showed statistically significant AGB differences compared to the species-specific models ($p < 0.05$). Measured WD showed 5%–10% less biomass than WD from databases and other sources and AGB was overestimated by up to 20% when using plot top height and underestimated by 8% using plot average height data rather than individual tree heights. The study concludes that biomass estimation in mangroves forests always benefit from species-specific models and individual tree measurements when appropriate input data are available. Tree level measurements from inventory plots play an important role for the improved estimation of forest biomass while scaling from individual trees up to the ecosystem level. Improved estimates of AGB will improve support our understanding of the productivity of mangrove forests, information that is needed for the long-term conservation of these fragile ecosystems that face many natural and anthropogenic pressures.

Data availability statement

The primary inventory data from the Bangladesh Sundarbans are available in TRY database (www.try-db.org/TryWeb/Home.php). The used semi-destructive sampling data for the Sundarbans is publicly available in the supplementary files of Mahmood *et al* (2019). The data that support the findings of this study are openly available at the following URL/DOI: 10.5281/zenodo.5544398 . Data will be available from 30 June 2022.

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Conflict of interest

The authors agreed that they have no conflict of interest.

Credit authorship contribution statement

Md Saidur Rahman: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing.

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Hossain Mahmood: data curation, writing—review and editing.

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